

Introduction

Flowering plants are the most successful and speciose group of land plants, and dominate most terrestrial biomes. Their success is due, in part, to an extraordinary diversity of mating systems that permits great flexibility in modes of reproduction. Indeed, even within a particular mating system, flexibility is emerging as a crucial element—so much so that the strict classification of breeding mechanisms into outbreeding, selfing (inbreeding) and asexual (apomictic) systems now appears far less clear-cut. The facultative nature of each of this classic trio of mating processes is now widely accepted and mixed mating systems are becoming recognized as the norm rather than the exception, as discussed by Barrett (2003) in the opening paper of this issue.

Recent approaches to the study of angiosperm mating systems have sought to determine the genetic, and ultimately molecular genetic, basis of their control and regulation, rather than simply to describe them. The aim of the Discussion Meeting on which this issue is based was to review and highlight recent molecular-based approaches to the study of mating system biology in plants.

The meeting was particularly timely in the light of the current general interest in gene flow in flowering plants that has arisen through concern and debate about the cultivation of genetically modified crops. Genes, including transgenes, can move through pollen and seed dispersal within and between populations of the same species, and less frequently between populations of different species. In angiosperms a variety of mating systems regulate pollen movement and also determine the amount of seed set (although they cannot, of course, affect seed dispersal). Any attempt to develop strategies to control the spread of transgenes must therefore require a thorough understanding of the way in which the various mating systems are regulated. Identification of genes that regulate mating, and thus gene flow, may also offer possibilities for manipulating the breeding systems of genetically modified crops in order to reduce or even eliminate gene flow through pollen. Development of apomictic seed producing crops is one potential route towards this goal, and is discussed in Richards (2003) and Spielman *et al.* (2003).

Throughout the meeting, the intention was always to explore angiosperm mating systems in their broadest sense, rather than simply to focus on those systems that are best understood at a molecular level, namely those regulating self-incompatibility (SI). Thus, to cover the breadth of variation in plant mating systems, but also convey a sense of the extent to which gene flow varies under these various mating systems, a structure was adopted for the meeting (and thus this issue) based on the concept of genomic fluidity, as follows.

- (i) The 'fluid genome' discusses sexual mating systems that regulate gene flow within and between populations of the same species (intraspecific gene flow). Such systems include well-characterized mechanisms that promote outbreeding, such as SI, heterostyly and dioecy. Over the past 10 years much progress has been made in analysing the molecular basis of various forms of SI and two papers are devoted exclusively to this topic, one discussing gametophytic SI (Franklin-Tong & Franklin 2003) and the other sporophytic SI (Hiscock & Tabah 2003). Less well-understood processes that regulate mating through the intimacy of pollen–pistil interactions are also covered—such as those interactions influencing pollen performance during its growth towards the ovule (Stephenson *et al.* 2003), and factors involved in the synchronization of developmental processes in pollen and ovary that are required for successful fertilization (Herrero 2003). Many mating systems include a degree of selfing and these are considered in terms of their evolution, their genetics and the effect they have on fitness (Charlesworth 2003). Finally, in this context, recent progress towards understanding the genetic basis of inbreeding depression is reviewed (Carr & Dudash 2003).
- (ii) The 'frozen genome' focuses on cases where no gene flow takes place between individuals because reproduction is asexual. Such apomictic or agamosperous modes of reproduction result in the production of fertile seed without fertilization and are found in a surprisingly wide range of flowering plants. An ability to 'fix' heterosis in this fashion, with the concomitant maintenance of seed quality, is an attractive commercial goal. A number of contributions focus not only on the various developmental processes that lead to agamospermy, but also its implications in terms of its evolution, maintenance and ecological impact (Van Dijk 2003).
- (iii) The 'invasive genome' describes aspects of interspecific gene flow in populations and factors that regulate it. A variety of mechanisms controlling interspecific incompatibility were explored with an emphasis on the unusual phenomenon of unilateral incompatibility, which appears to overlap mechanistically with SI. Other contributions (Abbott *et al.* 2003; Rieseberg *et al.* 2003; Comai *et al.* 2003) also addressed the consequences of interspecific gene flow with regard to hybridization, introgression, allopolyploid speciation and gene silencing.

The final paper by Norm Ellstrand forms a synoptic synthesis of past, present and future work on gene flow in flowering plants (Ellstrand 2003). He also makes predictions as to how such studies can inform rational debate on

One contribution of 21 to a Discussion Meeting Issue 'Mechanisms regulating gene flow in flowering plants'.

the extent to which transgenes may be expected to move between genetically modified crops and natural populations.

The last time that a meeting on plant breeding systems was held at The Royal Society was in 1974, when a Discussion Meeting entitled 'Incompatibility in flowering plants' was organized by Dan Lewis and Jack Heslop-Harrison. Speakers included pioneers of genetic and cell biological research on SI and pollen–pistil interactions: de Nettancourt, Linskens, Lundqvist and, of course, Lewis and Heslop-Harrison themselves. It was also the occasion on which Mike Lawrence gave his first account of the genetics of SI in poppy—work that ultimately led to the adoption of *Papaver rhoeas* as a 'model' system for the study of SI, and our current understanding of the molecular control of SI in poppy—discussed in detail in the contribution of Noni Franklin-Tong on mechanisms of gametophytic SI.

The relationship between SI and interspecific incompatibility, in the form of unilateral incompatibility (UI), was also discussed at the 1974 meeting and in this issue it is addressed in the paper by Hancock *et al.* (2003) that describes how it has been shown that molecules that regulate SI in tobacco also regulate some forms of UI in the genus *Nicotiana*.

The 1974 meeting explored the genetic basis of incompatibility systems as well as aspects of their cell biology, and inspired a generation of research into SI using the emerging methods of molecular genetic analysis. From the two reviews on SI presented here as part of the 'fluid genome' section, it is clear that these molecular approaches to SI research are not only clarifying the molecular mechanisms involved, but are also providing important paradigms for cell-to-cell interactions in plants. It is now vital to expand this field of research to bring an equivalent degree of molecular 'resolution' to the more challenging, but probably more important, aspects of mating systems, such as the bases of heterosis and inbreeding depression. Understanding these complex mechanisms will be essential if we are to provide food of sufficient quantity and quality to ensure our survival through the difficult decades ahead.

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